Ann. Zool. Fennici 46: 361–379 ISSN 0003-455X (print), ISSN 1797-2450 (online)
Helsinki 30 October 2009

Nest predation and nest defence in European and North American woodpeckers: a review

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Received 3 Sep. 2008, revised version received 8 Jan. 2009, accepted 13 Jan. 2009

Paclík, M., Misík, J. & Weidinger, K. 2009: Nest predation and nest defence in European and North American woodpeckers: a review. — *Ann. Zool. Fennici* 46: 361–379.

Birds that excavate their own cavities for breeding are traditionally considered to suffer little from nest predation. We reviewed the literature for nest predation rates, nest success, nest predator species and nest defence in European and North American woodpeckers. Predation rate varied from zero to 0.35 (median = 0.13, n = 33 populations), while nest success varied from 0.42 to 1.00 (median = 0.80, n = 84). Daily nest predation rate increased, while daily nest survival rate did not change with species body weight. This suggests a role of cavity entrance size in passive nest defence and differential causes of nest failure between small and large species. Twenty three predator species preyed upon woodpecker nests. Woodpeckers defended their nests by attacking the predators, blocking the cavity entrance, and by the selection of safe habitat/cavity and timing of breeding. We conclude by discussing gaps in the literature regarding woodpecker nest predation.

Introduction

Predation is generally considered to be the major cause of nest failure in birds, which makes it an important force in shaping bird behaviour and life-histories (Ricklefs 1969, Martin 1993). The risk of nest predation varies considerably among types of nests (Nice 1957, Martin 1993) as nests in cavities are less vulnerable to predation than are nests in open sites (Martin & Li 1992, Wesołowski & Tomiałojć 2005). Moreover, there is considerable variability in nest predation rates within each nesting guild. Among cavity nesters, species excavating their own cavities (primary cavity nesters) are reported to suffer less from predation than non-excavating species (Martin & Li 1992, Johnson & Kermott 1994).

Woodpeckers (family Picidae, subfamily Picinae) are typical primary cavity nesters as they excavate their own cavities for breeding, using trees, cacti, termitaria or the ground as a substrate (Del Hoyo *et al*. 2002). Woodpecker nests may be protected against predators in various ways. Cavities may physically prevent some predators from entering the nest (Kosinski & Winiecki 2004), and/or various woodpecker behaviours, such as timing of breeding (Ingold 1989), active nest defence (Li & Martin 1991), or habitat selection (Rolstad *et al*. 2000) may lower the risk of predation.

Nest predation in woodpeckers is traditionally considered one of the lowest in birds (Johnson & Kermott 1994, Martin & Li 1992, Martin 1995). However, only few woodpecker species/populations have been included in comparative studies and it is likely that much data have been accumulating in the literature since the mid-1990s. Moreover, woodpeckers represent a diverse group of birds, e.g. in terms of body size, geographical distribution and habitat selection (Del Hoyo *et al*. 2002), which complicates any generalizations about their susceptibility to nest predation. Recently, some vital rates of woodpecker populations (adult survival, nest success, recruitment rate) have been reviewed by Pasinelli (2006) and Wiebe (2006), but the issue of nest predation has received little attention. To better understand the nature of nest predation, the species identity of nest predators and bird responses to these predators need to be considered together with predation rates (Thompson 2007). Data on predators of woodpecker nests and nest defence have not been reviewed until now.

In this review, we collated and explored the published data on nest predation rates, nest success, nest predator species, and nest defence in European and North American woodpeckers. We also aimed to uncover potential weaknesses in the available data and make suggestions for further studies of nest success and predation in woodpeckers.

Material and methods

To obtain a comprehensive dataset, we searched internet databases (ISI Web of Science, Biological abstracts and Zoological record), using keywords such as "woodpecker" and "predation", and the scientific and English names of the main woodpecker genera. We also consulted the major books on woodpecker biology (Cramp 1985, Del Hoyo *et al*. 2002, Poole 2008). We restricted our search to European and North American woodpeckers.

The most desired variable searched for was predation rate, which is the simple proportion of nests that failed due to predation, taking all active nests with a known outcome as a basis for the calculation. Predation is defined here in a broader sense as any nest loss due to interactions with other animal species, including competition for cavities leading to nest failure (*see* Walters & Miller 2001). In studies that distinguish between competitive evictions and pure predation events, we used the desired overall predation rate and, separately, eviction rate for another analysis (*see* remarks in Appendix 1). From predation rate, we estimated daily predation rate (DPR) as follows:

$$\mathrm{DPR} = 1 - (1 - \mathrm{PR})^{1/0.5T} \qquad (1)$$

Instead of T (the length of the nesting cycle in days), we used a more realistic value of $0.5T$, assuming that nests were found on average in about half of their nesting cycle (Beintema 1996). T values (*see* Table 1) were calculated from midpoints of the intervals for the length of laying + incubation + fledgling periods reported by Del Hoyo *et al*. (2002). An exponent $1/T$ instead of $1/0.5T$ was included into the calculation of the daily predation rate (and daily survival rate, *see* below) in four studies with the majority of nests found during the early stage of the nesting cycle (LaBranche & Walters 1994, Pasinelli 2001, Mazgajski 2002, Fisher & Wiebe 2006a). The above calculation implies unrealistic constant survival probability over the entire nesting cycle (Shaffer & Thompson 2007), because almost all datasets were not sufficient to account for time dependence in nest survival.

Nest success is the proportion of nests producing at least one fledgling from all active nests (the exception was an estimate from DeLotelle & Epting [1992], where the number of cooperatively breeding groups [not number of active nests] was the counting unit). Published values were both the traditional nest success (simple proportion of successful nests/all nest found) and Mayfield nest success, which were treated separately in the database (*see* remarks in Appendix 1). We calculated simple proportions as an alternative to published Mayfield estimates (data by Li & Martin 1991, Conway & Martin 1993, Glue & Boswell 1994, and Smith 2005) to assure consistency across datasets. As a basis for the calculation, we used nests of a known outcome only (the exceptions were two estimates from Smith [2005] with nests of uncertain fate included).

Because the traditional nest success calculation is often biased (Mayfield 1975), we estimated the daily survival rate (DSR) from the traditional nest success values according to Beintema (1996) as follows:

$$\mathrm{DSR} = \mathrm{NS}^{1/0.5T} \tag{2}$$

For the published Mayfield estimates, we present the original daily survival rate calculated by the authors (*see* remarks in Appendix 1), but for analytical purposes, we calculated our own daily survival rate in the same way as in the rest of the studies. We performed a Spearman rank correlation of the published Mayfield daily survival rate estimates and our corrected daily survival rate calculations.

We obtained single estimates of the predation rate, daily predation rate, nest success and daily survival rate per population according to study location and period. If the same population was continually studied for more years, we pooled data across the years. In certain cases (in which authors did not estimate nest predation rate/nest success or calculated it by Mayfield or other methods different to ours; *see* above), we calculated or recalculated published estimates from the available data (for these calculated values *see* remarks in Appendix 1). Where data on more populations per species were available, we calculated an unweighted average across populations. For each population with an available predation rate and nest success, we estimated the proportion of nest losses caused by predation from all nest losses.

To test if the examined characteristics vary geographically, we compared the mean daily predation rate, daily survival rate, and the proportion of nest losses caused by predation between Europe and North America using the Mann-Whitney *U*-test, where the unweighted average for the species was the dependent variable in these analyses (n = number of species). Using a Spearman rank correlation, we correlated the daily pre-

Table 1. Woodpecker species included in the nest predation rate and nest success analyses in the present review. Nesting cycle lengths and body weights are given. Species from the same continent are shown in a decreasing order of body weight (data from Del Hoyo *et al.* 2002).

Species	Abbreviation	Length of the nesting cycle (days)	Body weight (g)
Europe			
Black woodpecker (*Dryocopus martius*)	BW	45	310
Eurasian green woodpecker (*Picus viridis*)	EGW	47	194
White-backed woodpecker (*Dendrocopos leucotos*)	W-bW	47	106
Great spotted woodpecker (*Dendrocopos major*)	GSW	39	81
Middle spotted woodpecker (*Dendrocopos medius*)	MSW	41	68
Eurasian three-toed woodpecker (*Picoides tridactylus*)	ET-tW	40	64
Lesser spotted woodpecker (*Dendrocopos minor*)	LSW	36	23
North America			
Pileated woodpecker (*Dryocopus pileatus*)	PW	45	295
Northern flicker (*Colaptes auratus*)	NF	45	135
Lewis's woodpecker (*Melanerpes lewis*)	LW	52	112
Acorn woodpecker (*Melanerpes formicivorus*)	AW	48	78
Red-headed woodpecker (*Melanerpes erythrocephalus*)	R-hW	44	77
Black-backed woodpecker (*Picoides arcticus*)	B-bW	39	75
Red-bellied woodpecker (*Melanerpes carolinus*)	R-bW	42	74
Hairy woodpecker (*Picoides villosus*)	HW	47	70
White-headed woodpecker (*Picoides albolarvatus*)	W-hW	45	65
American three-toed woodpecker (*Picoides dorsalis*)	AT-tW	41	56
Wiliamson's sapsucker (*Sphyrapicus thyroideus*)	WS	50	54
Yellow-bellied sapsucker (*Sphyrapicus varius*)	Y-bS	45	52
Red-naped sapsucker (*Sphyrapicus nuchalis*)	R-nS	45	49
Red-cockaded woodpecker (*Picoides borealis*)	R-cW	42	48

dation rate, daily survival rate, and the proportion of nest losses caused by predation with species body weight. Body weight may influence nest success in both directions — larger species may be more able to defend their nests physically, but they must build larger entrances to their cavities that are more accessible for larger and stronger predators. Body weights (*see* Table 1) were calculated as mid-points from the intervals reported by Del Hoyo *et al*. (2002). Finally, we analyzed the possible effects of the main "research effort" variable, the number of nests in a sample, on daily survival rate using a Spearman rank correlation test (n = number of all populations in all species). We evaluated whether studies based on fewer nests might provide different estimates of the daily survival rate, because smaller samples are associated with a lower precision of estimates (Beintema 1996).

Data on nest predators were divided into several classes according to the type of evidence: (1) predators directly observed or recorded by video while successfully robbing an active nest, and (2) predators identified indirectly from species-specific tracks left at the robbed nest. These signs include marks on the cavity-tree surface (e.g., broken cavity walls, claw and tooth marks), predator hair or feathers, and the appearance of egg and nestling remains (e.g., buried, thrown out, or broken eggs, chewed nestling feathers, partly eaten nestling bodies). We also included (3) predators mentioned in the original studies as "confirmed" but with no description of the predation event (*see* remarks in Appendix 2). We omitted notes on "potential" predators, which were generally defined as animals present at study plots and able to prey upon the nest, but without any direct or indirect evidence of this. We collected information on the prey species and items preyed upon (eggs, nestlings or adults attending the nest).

As a possible nest defence, we treated any behaviour that may potentially lower the risk of nest predation (Caro 2005). Included might be any observations of direct defence such as attacks on the predator or distraction displays, indirect behavioural mechanisms such as the selection of habitat associated with a lower predation risk, timing of breeding, and the role of accessibility of the cavity by predators (e.g., failed predation attempts). We did not consider self-defence of the young in nests.

Results and discussion

Nest predation rate and nest success

We gathered 33 estimates of the predation rate and the daily predation rate on 13 woodpecker species, of which six were European and seven North American. The predation rate varied from 0 to 0.35 (median = 0.13, mean = 0.15, SD = 0.11, n = 33; Appendix 1) and the daily predation rate varied from 0 to 0.019 (median = 0.005, mean = 0.007, SD = 0.006, n = 33). We gathered 84 estimates of nest success and the daily survival rate of 21 woodpecker species, of which 7 were European and 14 North American. Nest success varied from 0.42 to 1.00 (median = 0.80, mean = 0.78, SD = 0.13, n = 84; Table 2 and Appendix 1) and the daily survival rate varied from 0.959 to 1.000 (median = 0.990, mean = 0.988, SD = 0.009, n = 84). Our review revealed slightly higher nest predation rates than previous reviews, where the median predation rate varied from 0 to 0.07 (Johnson & Kermott 1994, Martin 1995; data on five woodpecker species). Although we support the view that nest predation is generally low in woodpeckers (*vs.* ≥ 0.5 in most open-nesting songbirds; Martin 1995), we point out that it is more variable than previously reported and rather high in some cases (0.35; Nilsson *et al*. 1991, Saab & Vierling 2001); the highest values of the nest predation rate included in the former reviews were 0.13 and 0.14 (Johnson & Kermott 1994, Martin 1995).

The proportion of nest losses caused by predation varied from 0.09 to 1.00 (median = 0.64, mean = 0.62, SD = 0.29, n = 31). Thus, predation was the principal cause of nest failure in woodpeckers similarly to birds in general (Ricklefs 1969, Martin 1995). For six species, we obtained eight estimates of the eviction rate that varied from 0.02 to 0.27 (median = 0.06, mean = 0.10, SD = 0.10, n = 8; *see* remarks in Appendix 1). The corresponding daily eviction rate varied from 0.001 to 0.015 (median = 0.003, mean = 0.005, SD = 0.006, n = 8). The proportion of nest losses due to eviction varied from 0.04 to 1.00

Table 2. Summary of predation rate (PR), daily predation rate (DPR), proportion of nest losses due to predation (LP), nest success (NS) and daily nest survival rate (DSR; *see* Material and methods for variable definitions) of European and North American woodpeckers. An unweighted mean across populations, range if available (in parentheses) and numbers of populations are given: n_1 refers to PR/DPR/LP, n_2 to NS/DSR. For species abbreviations *see* Table 1. Species from the same continent are shown in a decreasing order of body weight.

Species	PR	DPR	LP	n_1	NS	DSR	n_2
Europe							
BW	0.19 (0.02–0.35)	0.010 (0.001–0.019)	0.65 (0.24–1.00)	6	0.79 (0.55–0.96)	0.989 (0.974–0.998)	12
EGW	–	–	–	–	0.92	0.996	1
W-bW	0.27	0.013	0.64	1	0.82 (0.58–0.97)	0.991 (0.977–0.999)	5
GSW	0.14 (0.08–0.29)	0.007 (0.002–0.017)	0.61 (0.50–0.67)	4	0.82 (0.57–0.97)	0.990 (0.972–0.998)	9
MSW	0.07 (0.05–0.09)	0.003 (0.002–0.004)	0.28 (0.09–0.40)	3	0.77 (0.42–0.90)	0.987 (0.959–0.995)	6
ET-tW	0.08	0.004	0.38	1	0.76 (0.75–0.79)	0.987 (0.986–0.988)	3
LSW	0.04	0.002	0.19	1	0.79 (0.74–0.84)	0.987 (0.983–0.990)	3
North America							
PW	–	–	–	–	0.83	0.992	1
NF	0.18 (0.00–0.33)	0.009 (0.000–0.018)	0.84 (0.69–1.00)	6	0.72 (0.50–1.00)	0.985 (0.970–1.000)	10
LW	0.26 (0.16–0.35)	0.012 (0.007–0.016)	0.86 (0.82–0.90)	2	0.75 (0.57–0.85)	0.988 (0.979–0.994)	3
AW	0.18 (0.09–0.27)	0.008 (0.004–0.013)	0.66 (0.32–1.00)	2	0.80 (0.73–0.92)	0.991 (0.987–0.997)	4
R-hW	–	–	–	–	0.76 (0.69–0.80)	0.987 (0.983–0.990)	4
B-bW	–	–	–	–	0.82 (0.69–1.00)	0.989 (0.981–1.000)	4
R-bW	–	–	–	–	0.67 (0.47–0.82)	0.980 (0.965–0.991)	3
HW	0.18 (0.13–0.22)	0.008 (0.006–0.011)	1.00 (1.00–1.00)	2	0.83 (0.78–0.88)	0.992 (0.989–0.995)	2
W-hW	–	–	–	–	0.86 (0.83–0.88)	0.993 (0.992–0.994)	2
AT-tW	–	–	–	–	0.66 (0.53–0.79)	0.982 (0.970–0.994)	2
WS	0.01	0.001	0.50	1	0.98	0.999	1
Y-bS	0.13	0.006	0.25	1	0.60 (0.50–0.70)	0.977 (0.970–0.984)	2
R-nS	0.04 (0.00–0.10)	0.002 (0.000–0.005)	0.49 (0.48–0.50)	3	0.91 (0.80–1.00)	0.996 (0.990–1.000)	3
R-cW	–	–	–	–	0.75 (0.66–0.84)	0.987 (0.980–0.994)	4

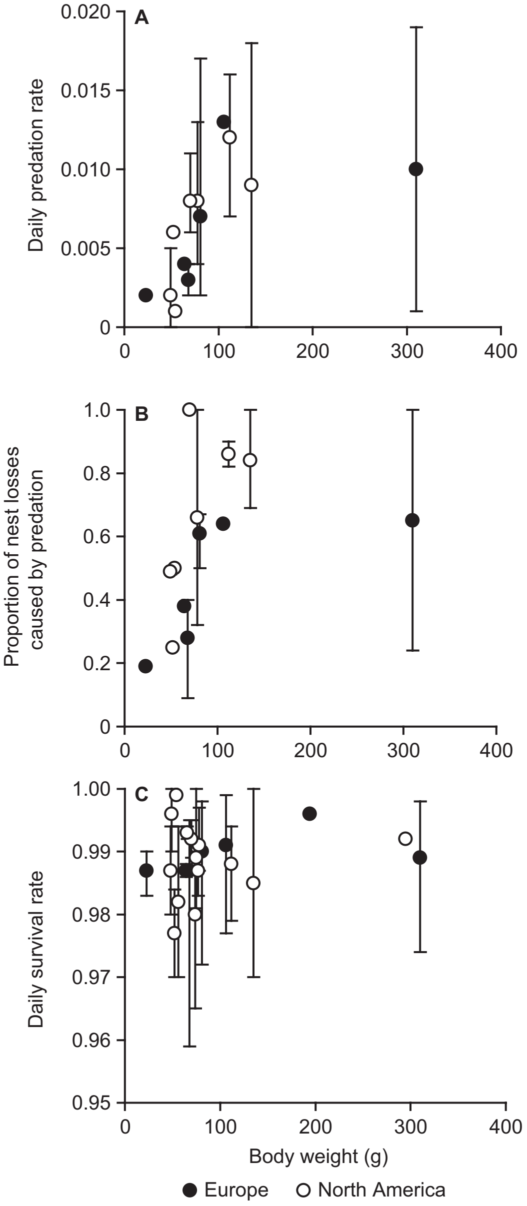

Fig. 1. The effect of body weight on (**A**) the daily nest predation rate, (**B**) the proportion of nest losses caused by predators, and (**C**) the daily nest survival rate. Shown is an unweighted average across populations (circles) and a range of estimates (whiskers) for each species. North American (open circles) and European species (filled circles) are distinguished.

(median = 0.29, mean = 0.39, SD = 0.35, $n = 8$), which suggests that competitive eviction is sometimes more important than pure predation. In this respect, cavities may be safe against predators, but attractive to other cavity nesting species, suggesting possible contradictory selection pressures on woodpecker breeding (Nilsson 1984).

The literature showed considerable variability in all examined characteristics among species — predation rate, daily predation rate, proportion of nest losses caused by predation, nest success and daily survival rate — yet the amount and sources of this variation are difficult to quantify because of differences in sample sizes (Table 2). Both daily predation rate ($r_s = 0.87$, $p_{\text{exact}} < 0.001$, $n = 13$; Fig. 1A) and proportion of nest losses caused by predation ($r_s = 0.75$, $p_{\text{exact}} = 0.004$, $n = 13$; Fig. 1B) correlated significantly positively with body weight (23 to 310 g), but body weight did not correlate with daily survival rate ($r_s = 0.20$, $p = 0.389$, $n = 21$; Fig. 1C). Larger species suffered more from predation than smaller species, possibly because larger entrances make their cavities accessible to more predator species (*see* below; Wesołowski 2002). Given that daily survival rate did not change with species body weight, our results suggest differential causes of nest failure between small and large species. Daily predation rates, daily survival rates, and proportions of nest losses caused by predation did not differ between the European and North American species (daily predation rate: $p_{\text{exact}} = 0.976$, daily survival rate: $p_{\text{exact}} = 0.868$, proportion of nest losses caused by predation: $p_{\text{exact}} = 0.181$; for data *see* Table 2).

Predators

At least 23 animal species were identified as predators of woodpecker nests, of which 7 were European and 17 North American (including the introduced European starling [*Sturnus vulgaris*]); they comprised 1 reptile, 8 bird and 14 mammal species (Appendix 2). The number of known predators is lower for woodpeckers as compared with that for open nesters (Thompson 2007). This is partly a consequence of a lower sampling effort (Weidinger 2008) in woodpecker studies (number of studied species, small sample sizes). Nevertheless, the number of potential predators is, in fact, lower in cavity nesters, as it is constrained by the size of cavity entrances. From the main classes of predators, arboreal snakes are regular predators of bird nests in North America rather than in Europe and their importance varies with latitude (Thompson 2007). Birds are competitors of woodpecker nests rather than typical predators, because corvids, the principal avian predators of open nests (Thompson 2007, Weidinger 2009) cannot usually enter cavities. Only one corvid species, the jackdaw (*Corvus monedula*), was recorded to usurp black woodpecker (*Dryocopus martius*) cavities (Nilsson *et al*. 1991). Some woodpecker species regularly prey upon nests of other woodpeckers (present review) as well as upon other cavity (Nilsson 1984, Walankiewicz 2002) and open nests (Hazler *et al*. 2004, Weidinger 2009). Mammals, especially carnivores and rodents, are in general important predators of bird nests (Thompson 2007, Adamík & Král 2008, Weidinger 2009).

The main difference in predator communities between cavity and open nesters is a group of specialised competitors for nest sites, which are not apparently dangerous to open nesters (Lindell 1996). Six species could be classified as nest competitors (that destroy nests) in the present review — the European starling, redstart (*Phoenicurus phoenicurus*), house wren (*Troglodytes aedon*), jackdaw, the European red squirrel (*Sciurus vulgaris*), and the red squirrel (*Tamiasciurus hudsonicus*). These animals did not always eat the nest content (although both squirrel species could do so; Walankiewicz 2002), but usually buried it with material brought to the nest (sticks, leaves) or threw out the nest content and then nest in the usurped cavity (Shelley 1935, Howell 1943, Short 1979, Lange 1996, Walters & Miller 2001, Wiebe 2003). However, it is difficult to clearly distinguish among pure predators and nest competitors, because reasons for destroying nests (food/nest site) seem to be mixed in some species (particularly in non-carnivorous mammals). Only starlings frequently usurp freshly excavated woodpecker cavities before woodpeckers start laying (Ingold 1989).

The literature showed that nests were preyed upon at various stages of a nesting cycle; predators took both eggs and nestlings, but only rarely the incubating or brooding adults (Appendix 2). Qualitative data do not permit the evaluation of whether some predators prefer nests at a certain stage. Of the frequently recorded predators, the deer mouse (*Peromyscus maniculatus*) preyed upon only nests with eggs, while carnivores mostly took nestlings (except European species of martens [*Martes* sp.] depredating black woodpecker nests with eggs). In the British Columbian northern flicker population, starlings and squirrels almost exclusively preyed upon eggs (Fisher & Wiebe 2006a, K. L. Wiebe pers. comm.). The red squirrel (Howell 1943) and the European starling (Shelley 1935) were once reported to kill adult woodpeckers, but only carnivores are known to kill adults regularly (Appendix 2).

Predators substantially larger than woodpeckers cannot pass the cavity entrance. To prey upon a nest, they must break cavity walls to reach the nest content and this generally happens in decaying or dead trees. This behaviour was reported for the great spotted woodpecker (*Dendrocopos major*; Tracy 1933, Brown 1976), marten (Misík & Paclík 2007), raccoon (*Procyon lotor*; Kilham 1971), black bear (*Ursus americanus*; DeWeese & Pillmore 1972, Franzreb & Higgins 1975, Walters & Miller 2001) and the domestic cat (*Felis cattus*; Dennis 1969).

Nest defence

Woodpeckers may avoid nest predation by selecting a safe habitat at various spatial scales (forest stand, tree, and cavity) as they are not limited by the location of previously existing cavities. However, excavating ability varies among species (Martin 1993) as it is limited by tree hardness (Schepps *et al*. 1999). At the scale of entire forest blocks, Norwegian black woodpeckers selected isolated large trees retained in clear-cuts, where they were less susceptible to predation by pine marten (*Martes martes*) than in contiguous old-growth forest stands (Rolstad *et al*. 2000). In British Columbia, northern flickers (*Colaptes auratus*) faced a trade-off between the risk of predation and competitive eviction, given that cavities associated with conifers were more likely to be preyed upon by mammals but less likely to be usurped by starlings (Fisher & Wiebe 2006a).

For predators, there may be some barriers to locate and/or approach the cavity, e.g. height above ground. In British Columbia, northern flicker cavities located higher up were less often preyed upon, but height above ground did not influence the probability of eviction (Fisher & Wiebe 2006a). The success of cavity nests often increases with height above ground (Nilsson 1984, Evans *et al*. 2002) and cavity nesters are known to compete for higher cavities (Nilsson 1984). The behaviour of the red-cockaded woodpecker (*Picoides borealis*) is unique — it injures the bark of the nest tree because the fresh resin makes the trunk unsuitable for climbing by snakes (Jackson 1974, Conner *et al*. 2004). Also, concealment may influence the risk of predation: better concealed (by vegetation around the entrance) northern flicker cavities in British Columbia were less preyed upon by mammals (Fisher & Wiebe 2006a). In Sweden, black woodpecker nests in new cavities were less preyed upon than those in old cavities (Nilsson *et al*. 1991), presumably because local predators memorized the location of old cavities, while new cavities had to be discovered first (Sonerud 1989). A similar pattern was reported for northern flickers in British Columbia, but not for three populations of the great spotted woodpecker (twice no effect of cavity age in Poland and Russia, once a reverse pattern in Great Britain; *see* Wiebe *et al*. 2007). Given that woodpecker populations reuse cavities to varying degrees, cavity excavation/reuse may have various benefits and costs that vary according to the ecological context (Wiebe *et al*. 2007). Although switching of nest sites under the outcome of previous breeding or possible encounters with a predator slightly before breeding may be a passive defence, it has not lead to reproductive benefits in the British Columbian population of northern flickers (Fisher & Wiebe 2006c).

Once discovered by a predator, some cavities are still safer from depredation than others due to their internal shape and dimensions. In particular, narrow cavity entrances may prevent large predators from entering the nest. For example, the pine marten could easily enter black woodpecker cavities with an oval entrance of 7 × 12 cm (Rolstad *et al*. 2000, Nilsson *et al*. 1991), but not great spotted woodpecker cavities with a 4.5 cm diameter entrance (Kosinski & Winiecki 2004, Misík & Paclík 2007). Similarly, the European starling failed to prey upon nests of the smaller downy woodpecker (*Picoides pubescens*) due to a narrow entrance (Howell 1943). In the present review, we showed that daily predation rate was positively correlated with body size (~ entrance diameter) across species (*see* above; Fig. 1). To reach the nest without entering the cavity, large predators try to capture nestlings by paws (or break the cavity walls; *see* below). For this reason, the selection of deep cavities by woodpeckers may lower the risk of predation — e.g. large cavities of northern flickers in British Columbia were preyed upon less often than small cavities (Fisher & Wiebe 2006a). In comparison to other cavity nesters, woodpecker cavities are usually deeper and without a nest lining (Del Hoyo *et al*. 2002), which potentially increases nest safety because predators may try to reach the brood by pulling out the nest material (Walankiewicz 2002).

According to the reviewed literature, some large predators repeatedly failed to prey upon woodpecker nests due to inaccessibility, although they were successful in breaking cavity walls in other cases. In British Columbia and California, black bears repeatedly gave up trying to prey upon arctic three-toed woodpecker (*Picoides arcticus*), hairy woodpecker (*Picoides villosus*), yellow-bellied sapsucker (*Sphyrapicus varius*), red-naped sapsucker (*Sphyrapicus nuchalis*) and northern flicker nests (Dixon 1927, Erskine & McLaren 1972, Walters & Miller 2001), while pine martens in Poland were unable to prey upon great spotted woodpecker nests (Kosinski & Winiecki 2004). Low predation by the black bear on the red-naped sapsucker may be due to frequent nesting in living trees, contrary to the northern flicker that often breeds in dead trees and suffers more from predation (Walters & Miller 2001). In New Hampshire, a raccoon failed to prey upon a hairy woodpecker nest in one case (Kilham 1968), but in another case a raccoon captured a brooding adult of the yellow-bellied sapsucker, being apparently unable to reach the nestlings (Kilham 1977b). Thus, selection of living trees with resistant wood may lower the risk of nest predation by physically strong predators.

Proper timing of breeding may act as an indirect nest defence mechanism as nests later in the season are less vulnerable to eviction by a simultaneously breeding competitor, the European starling (Ingold 1989, Wiebe 2003, Smith 2005). In Mississippi, 52% of fresh empty cavities of the red-bellied woodpeckers, a species that breeds at the same time as the starling, were usurped before egg-laying. In the same-sized but later-breeding red-headed woodpecker, only 7% of cavities were usurped by starlings (Ingold 1989). However, the advantage of delayed breeding is compromised by the lowered fecundity and re-nesting potential of late broods (Ingold 1996, Wiebe 2003), and there may be other reasons of nest failure that does not change with date in the same way (e.g. mammalian predation; Fisher & Wiebe 2006a).

Direct behavioural responses to the presence of a predator in close proximity to the nest included chasing or attacking the intruder (18 published anecdotal events + 2 experimental studies, 11 woodpecker species × 9 predator species), and entering the nest with increased attentiveness (one anecdotal event [male hairy woodpecker against young red squirrels crawling the nest tree; Kilham 1968] + 2 experimental studies, 2 woodpecker species × 2 predator species). However, published anecdotal observations of woodpecker behaviour suggest rather than confirm an active nest defence. Only two experiments have been performed to date — in the first, nesting northern flickers in British Columbia presented with models of the European starling and the yellow-headed blackbird (*Xanthocephalus xanthocephalus*) intensively defended against the starling model by dives, direct attacks, and increased nest-attentiveness (Wiebe 2004). Similar behaviours performed against models of the red squirrel were observed in the second experiment, where yellow-headed blackbird and cedar waxwing (*Bombycilla cedrorum*) models were used as controls (Fisher & Wiebe 2006b). Two anecdotal observations from Colorado (Crockett & Hansley 1977) suggest a possible interaction between nest height and efficiency of active nest defence. A higher cavity (10 m above ground) of the Williamson's sapsucker (*Sphyrapicus thyroideus*) was successfully defended against the long-tailed weasel (*Mustela frenata*), but a lower cavity (1.8 m) was not; in both cases birds intensively attacked the predator. "Blocking" of the cavity entrance by parent hairy woodpeckers in New Hampshire and by northern flickers in British Columbia may also be an example of a combined direct and indirect defence strategy (Kilham 1968, Fisher & Wiebe 2006b). A response to humans (adult pileated woodpecker [*Dryocopus pileatus*] attacked researcher's hand; Hoyt 1957) suggests possible direct defence against large predators.

Methodological considerations

We identified several weaknesses in the reviewed data on woodpecker breeding success, nest predators and nest defence. Generally, the number of studies reporting nest success in woodpeckers is low as compared with other cavity and open nesters, and less than half of these studies provided estimates of predation rate (*see* Nice 1957, Ricklefs 1969, Johnson & Kermott 1994, Martin 1995, Wesołowski & Tomiałojć 2005). This precludes detailed quantitative comparisons among species, habitats and geographical areas. Taking that the precision of nest success estimates critically depends on sample size, i.e., the number of nests (Beintema 1996), most reviewed studies were based on inadequate sample sizes (from eight to 1303 nests, median = 35, mean = 107, SD = 229, n = 81 study populations). We found a significant positive correlation between the number of nests in a sample and daily survival rate estimate ($r_s = 0.23$, $p = 0.041$, $n = 81$; Fig. 2). This may be because daily survival rate estimates based on smaller samples are more sensitive to the number of recorded nest failures that are rare in woodpeckers. Woodpecker populations were studied from 1 to 58 years (median = 6, mean = 10, SD = 13, n = 54) and the number of nests studied per year varied from 1 to 156 (median = 9, mean = 17, SD = 28, n = 54). Annual estimates of breeding success usually differ (e.g. Pasinelli 2001, Wiktander *et al*. 2001) due to multiple reasons and, therefore, estimates based on single-year data may not be representative of the studied population.

The interpretability of nest success estimates depends on the method of data analysis (Weidinger 2007). Only 17 estimates of nest success (< 21% of the reviewed data) from 9 studies

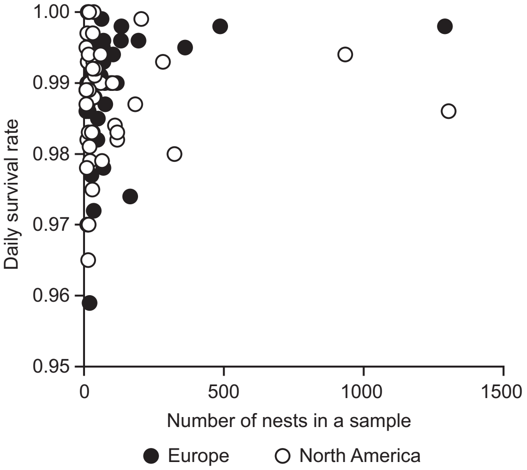

Fig. 2. Correlation between daily survival rate and the number of nests in a sample ($n = 81$ study populations, all species). North American (open circles) and European species (filled circles) are distinguished.

(Li & Martin 1991, Glue & Boswell 1994, LaBranche & Walters 1994, Dobbs *et al*. 1997, Leonard 2001, Saab & Vierling 2001, Smith 2005, Fisher & Wiebe 2006a, Kosinski & Ksit 2006) were based on some variant of the Mayfield method (Mayfield 1975). The remaining studies were based on the traditional method, which often overestimates true nest success. We took this into account and corrected these traditional estimates as suggested by Beintema (1996). The 16 cases of Mayfield daily survival rate estimates were highly correlated with the corrected daily survival rate used by us ($r_s = 0.92$, $p_{exact} < 0.001$, $n = 16$). Nevertheless, this solution is not ideal, because even Mayfield estimates assume a constant daily survival rate, while nest losses may accumulate in a certain period of the nesting cycle (e.g., laying and incubation; Fisher & Wiebe 2006a). Thus, we urge researchers to implement the recently developed methods of nest survival analysis that account for time-dependent covariates of nest survival (Shaffer & Thompson 2007). To our knowledge, there is only one application of such methods to woodpecker data (Fisher & Wiebe 2006a).

Our list of woodpecker nest predators (Appendix 2) is likely to be incomplete due to a limited sampling effort (Weidinger 2008) and the general difficulty in observing predators in the field. Videotaping is currently the most reliable method of nest predator identification and is being routinely used in studies of open passerine nests (Thompson 2007, Weidinger 2008). In contrast, most data on predators of woodpecker nests are based on indirect cues such as the appearance of preyed-upon nests. Nest predators were directly observed (mostly anecdotally) in only eight studies and just a single study implemented video surveillance (Fisher & Wiebe 2006a). We encourage the wider use of video surveillance in woodpecker studies to obtain both qualitative and quantitative data on nest predators. Based on the available indirect data, only tentative conclusions can be drawn about the dominant nest predators in some woodpecker populations — e.g. pine marten *vs*. black woodpecker in Scandinavia (Nilsson *et al*. 1991, Rolstad *et al*. 2000) and European starling *vs*. great spotted woodpecker in Great Britain (Smith 2005).

Published qualitative notes on direct nest defence included mostly reports of chasing and attacking the predator, probably because such behaviour is easy to detect (birds are often calling) and observe. Hiding or attending the nest by parents is much less obvious and the frequency of such behaviour might be underestimated (compared to experimental studies; Wiebe 2004, Fisher & Wiebe 2006b). Li and Martin (1991) suggested that the larger body size of woodpeckers compared with many non-excavating species increases the ability to directly defend the nest. However, while observational studies may not reveal the mechanisms underlying the observed patterns, all but two (Wiebe 2004, Fisher & Wiebe 2006b) experimental studies of nest defence were performed on open or secondary cavity nesters. Experiments on large *vs*. small woodpecker species should be particularly informative, because these two groups differ both in nest defence potential and nest predation rates.

Management implications

European and North American woodpeckers are, in general, not globally threatened (although they may be declining at the national scale; *see* Mikusiński & Angelstam 1997, Del Hoyo *et al*. 2002) with the exceptions of the ivorybilled woodpecker (*Campephilus principalis*; critically endangered), red-cockaded woodpecker (vulnerable) and the red-headed woodpecker (near threatened; IUCN 2008). None of these woodpecker species is documented to be threatened by predation (Del Hoyo *et al*. 2002, IUCN 2008). A prime example of suggested, but undocumented, threat is the invasion of the introduced European starling across North America, which was widely expected to have a detrimental effect on native woodpecker populations due to nest evictions. Although starlings negatively affected reproductive success (e.g., red-bellied woodpecker; Ingold 1989) or even caused a local population decline of woodpeckers (gila woodpecker; Kerpez & Smith 1990), long-term population monitoring did not reveal such a negative effect at the continental scale (Koenig 2003). In Great Britain, long-term population decline in the European starling coincided with an increase in great spotted woodpeckers (Smith 2005), but the causality of this relationship remains unclear.

The conservation of woodpeckers mostly deals with habitat management (Conner & Rudolph 1991, Mikusiński & Angelstam 1997, Wesołowski *et al*. 2005, Bull *et al*. 2007). In the red-cockaded woodpecker, competition (not "predation" as defined in the present review) with pileated woodpeckers that frequently enlarge empty red-cockaded woodpecker cavities is taken as a serious threat (IUCN 2008). The exclusion of fire in mature pine forests in the south-eastern United States increased the abundance of dead wood and, consequently, that of pileated woodpeckers (Conner *et al*. 2004). Management involves fitting restrictor plates to cavities or making artificial cavities (Carter *et al*. 1989, Allen 1991, IUCN 2008) but, ultimately, increased competition is linked to habitat change, which should be taken as a priority for management (Conner *et al*. 2004).

Little is known about the demographic consequences of nest predation in general, even in bird species exposed to high predation pressures, and attempts to reduce predation yielded mixed results (*see* Gibbons *et al*. 2007). Because nest predation is comparatively low in woodpeckers, there seems to be low potential for a significant effect of nest predation on woodpecker populations, and, consequently, low potential for the effective conservation of woodpeckers through management of their nest predators.

Acknowledgements

This work was supported by the Faculty of Education of the Palacký University Olomouc (IGS 11417091), Ministry of Education of the Czech Republic (MSM 6198959212), and by the Czech Science Foundation (GACR 206/07/0483). We would like to thank Peter Adamík, Jiří Reif, Paul Rawsthorne, the reviewers Karen L. Wiebe and Matthew Schlesinger, and the editor Johan Kotze for valuable comments on the manuscript.

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Appendix 1. Literature data on nest predation rate and nest success, and calculated data on daily nest predation rate, proportion of nest losses due to predation, and daily nest survival rate in European and North American woodpeckers (for species abbreviations and variable codes *see* Table 1). Numbers of nests, geographical location, study period and additional data on published Mayfield estimates of nest success and estimates of eviction rates are given. Species from the same continent are shown in a decreasing order of body weight and data on the species are shown in a decreasing order of daily nest survival rate.

Species	PR	DPR	LP	NS	DSR	*n* (nests)	Location	Period	Source
Europe									
BW				0.96[a]	0.998	134	Germany	1978–1989	Lang & Rost (1990)
				0.92	0.996	25	France	1966–1981	Pasinelli (2006)
	0.02[a]	0.001	0.24[a]	0.91	0.996	194	Germany	1974–1993	Lange (1996)
				0.88	0.994	43	Germany	1977–1978	Lang & Rost (1990)
				0.86	0.993	70	Germany	1976–1978	Pasinelli (2006), Lang & Rost (1990)
	0.15	0.007	1.00[a]	0.85[a]	0.993	13	Sweden	1985–1990	Tjernberg *et al.* (1993)
				0.80[a]	0.990	117	Denmark	1982–1999	Christensen (2002)
				0.80[a]	0.990	96	Denmark	1977–1986	Johansen (1989)
	0.29	0.015	1.00[a]	0.71[a]	0.985	49	Sweden	1985–1990	Tjernberg *et al.* (1993)
	0.08[a]	0.004	0.25	0.67[a]	0.982	48	Germany	1977–1983	Von Kühlke (1985)
	0.35[a]	0.019	0.89[a]	0.61[a]	0.978	69	Sweden	1986–1988	Nilsson *et al.* (1991)
	0.03[a,c]	0.001[c]	0.07[a,c]						
	0.24[a]	0.012	0.53[a]	0.55[a]	0.974	165	Norway	1990–1995	Rolstad *et al.* (2000)
EGW				0.92[a]	0.996	132	G. Britain	1939–1989	Glue & Boswell (1994)
				0.85[b]	0.996[a,b]	252			
W-bW				0.97[a]	0.999	62	Finland	1970–1991	Virkkala *et al.* (1993)
				0.91	0.996	70	Norway	1988–1994	Pasinelli (2006)
				0.84	0.993	30	France		Pasinelli (2006)
				0.78[a]	0.989	9	Norway	1966–1979	Bringeland & Fjære (1981)
	0.27[a]	0.013	0.64[a]	0.58[a]	0.977	26	Poland	1990–1991	Wesołowski (1995)
GSW				0.97[a]	0.998	487	G. Britain	1984–2003	Smith (2005)
				0.91[a,b]	0.998[a,b]				
				0.97[a]	0.998	1290	G. Britain	1943–2000	Smith (2005)
				0.86[a,b]	0.996[a,b]				
				0.91[a]	0.995	361	G. Britain	1939–1989	Glue & Boswell (1994)
				0.84[b]	0.996[a,b]	732			
	0.09[a]	0.002*	0.60[a]	0.81	0.995*	32	Poland	1996–1998	Mazgajski (2002)
	0.08[a]	0.004	0.67	0.89	0.994	104	Poland	2002–2004	Kosinski & Ksit (2006)
	0.08[a,c]	0.004[c]	0.67[c]						
				0.82[b]	0.995[b]	88			
	0.08[a]	0.004	0.50[a]	0.84[a]	0.991	25	Poland	2002–2004	Mazgajski & Rejt (2006)
				0.78	0.987	14	Sweden		Pasinelli (2006)
				0.64	0.977		Russia		Michalek & Miettinen (2003)
	0.29[a]	0.017	0.67[a]	0.57	0.972	35	G. Britain		Michalek & Miettinen (2003)
	0.26[a,c]	0.015[c]	0.60[a,c]						
MSW				0.90	0.995	38	Austria		Pasinelli (2006)
				0.90	0.995	68	Russia		Pasinelli (2006)
	0.09[a]	0.002*	0.34[a]	0.74	0.993*	35	Switzerland	1992–1996	Pasinelli (2001)
	0.07[a]	0.004	0.40	0.83	0.991	59	Poland	2002–2004	Kosinski & Ksit (2006)
	0.07[a,c]	0.004[c]	0.40[c]						
				0.69[b]	0.991[b]	50			
				0.82[a]	0.990	11	Germany	1998–2001	Wirthmüller (2002)
	0.05[a]	0.002	0.09[a]	0.42	0.959	19	Sweden	1975–1982	Pettersson (1985)
ET-tW	0.08[a]	0.004	0.38[a]	0.79	0.988	38	Germany	1993–2004	Pechacek (2006)

continued

Appendix 1. Continued.

Species	PR	DPR	LP	NS	DSR	*n* (nests)	Location	Period	Source
				0.75[a]	0.986	16	Switzerland	1966, 1969–1970	Von Ruge (1974)
				0.75[a]	0.986	8	Switzerland	1991–1998	Von Ruge *et al.* (2000)
LSW				0.84[a]	0.990	74	G. Britain	1939–1989	Glue & Boswell (1994)
				0.83[b]	0.995[a,b]	129			
	0.04[a]	0.002	0.19[a]	0.79[a]	0.987	76	Sweden	1989–1998	Wiktander *et al.* (2001)
				0.74	0.983	31	Germany		Pasinelli (2006)
North America									
PW				0.83	0.992		Oregon		Martin (1995)
NF	0.00[a]	0.000	-	1.00[a]	1.000	34	Arizona	1987–1989	Li & Martin (1991)
				1.00[b]	1.000[b]				
	0.14	0.007	1.00	0.86	0.993	14	Wisconsin		Johnson & Kermott (1994)
	0.13[a]	0.006	0.75[a]	0.83[a]	0.992	48	Massachusetts	1960, 1969	Dennis (1969)
	0.02[c]	0.001[c]	0.13[a,c]						
				0.79[a]	0.990	19	Ohio	1921-39	Kendeigh (1942)
	0.20	0.005*	0.75[a]	0.73	0.986*	1303	B. Columbia	1998–2007	K. L. Wiebe pers. comm.
	0.05[c]	0.002[c]	0.17[a,c]						
				0.51[a,b]	0.985[b]	662	B. Columbia		Fisher & Wiebe (2006a)
				0.67[a]	0.982	119			Wiebe & Moore (2008)
	0.33	0.018	1.00	0.67	0.982	12	Wisconsin		Wiebe & Moore (2008)
				0.62	0.979	21	B. Columbia	1958–1959	Johnson & Kermott (1994)
	0.30[a]	0.016	0.69[a]	0.57[a]	0.975	30	B. Columbia	1989–1994	Walters & Miller (2001)
				0.50	0.970	12	Colorado		Johnson & Kermott (1994)
LW				0.85	0.994		Wyoming		Tobalske (1997)
	0.16	0.007	0.90	0.83[a]	0.993	283	Idaho	1994–1997	Saab & Vierling (2001)
				0.78[b]	0.995[b]				
	0.35[a]	0.016	0.82[a]	0.57[a]	0.979	65	Colorado	1992–1993	Saab & Vierling (2001)
	0.02[c]	0.001[c]	0.04[a,c]	0.46[b]	0.985[b]				
AW				0.92[a]	0.997	12	Arizona	1987–1989	Li & Martin (1991)
				0.88[b]	0.997[b]				
				0.82[a]	0.992	45	N. Mexico	1975–1977	Stacey (1979)
	0.27[a]	0.013	1.00[a]	0.74[a]	0.988	34	California	1968–1974	Troetschler (1976)
	0.27[c]	0.013[c]	1.00[a,c]						
	0.09[a]	0.004	0.32[a]	0.73	0.987	183	California		Johnson & Kermott (1994)
R-hW				0.80[a]	0.990	59	Mississippi	1985–1987	Ingold (1989)
				0.78	0.989	18	Mississippi		Johnson & Kermott (1994)
				0.75	0.987	8	Colorado		Johnson & Kermott (1994)
				0.69	0.983	16	Mississippi	1984–1987	Ingold (1990)
B-bW				1.00	1.000	14	Wyoming		Dixon & Saab (2000)
				0.87	0.993	33	Idaho		Dixon & Saab (2000)
				0.71[a]	0.983	28	Montana		Dixon & Saab (2000)
				0.69	0.981	19	Oregon		Dixon & Saab (2000)
R-bW				0.82	0.991	38	Mississippi		Johnson & Kermott (1994), Martin (1995)
				0.71[a]	0.984	110	Mississippi	1985–1987	Ingold (1989)
				0.47	0.965	15	Illinois		Johnson & Kermott (1994)

continued

Appendix 1. Continued.

Species	PR	DPR	LP	NS	DSR	*n* (nests)	Location	Period	Source
HW	0.13	0.006	1.00[a]	0.88[a] 0.76[b]	0.995 0.993[b]	8	Arizona	1987–1989	Li & Martin (1991), Martin (1995)
	0.22[a]	0.011	1.00[a]	0.78[a]	0.989	9	B. Columbia	1989–1994	Walters & Miller (2001)
W-hW				0.88	0.994	16	Oregon		Garrett *et al.* (1996)
				0.83	0.992	41	Oregon		Garrett *et al.* (1996)
AT-tW				0.79[b]	0.994[b]	60	Montana, Idaho		Leonard (2001)
				0.53	0.970	15	Oregon		Leonard (2001)
WS	0.01[a]	0.001	0.50[a]	0.98[a] 0.96[b]	0.999 0.999[b]	204	Arizona		Li & Martin (1991), Martin (1995), Dobbs *et al.* (1997)
Y-bS				0.70[a]	0.978	10	N. Hampshire	1967	Kilham (1971)
	0.13[a]	0.006	0.25[a]	0.50[a]	0.970	16	N. Brunswick		Erskine & McLaren (1972)
R-nS	0.00[a]	0.000	-	1.00[a] 1.00[b]	1.000 1.000[b]	18	Arizona	1987–1989	Li & Martin (1991)
	0.03[a]	0.001	0.50[a]	0.94[a]	0.997	31	Montana	1990–1991	Tobalske (1992)
	0.10[a]	0.005	0.48[a]	0.80[a]	0.990	103	B. Columbia	1989–1994	Walters & Miller (2001)
R-cW				0.78[a] 0.73[b]	0.994* 0.994[b]	934	N. Carolina	1980–1985	LaBranche & Walters (1994)
				0.84[a]	0.992	31	Florida	1980–1987	DeLotelle & Epting (1992)
				0.70	0.983	118	S. Carolina		Johnson & Kermott (1994)
				0.66	0.980	324	Georgia		Johnson & Kermott (1994)

[a] Own calculation according to variable definitions in this review (*see* Material and methods). All "traditional" DSR/DPR estimates (not denoted) were calculated as $DPR = 1 - (1 - PR)^{1/0.5T}$ and $DSR = NS^{1/0.5T}$ (T = the length of the nesting cycle; for data *see* Table 1). A different exponent $1/T$ (instead of $1/0.5T$) was included in the calculation of DPR/DSR in four studies with the majority of nests found in the early stage of the nesting cycle (denoted by asterisks).

[b] Mayfield estimate of NS/DSR.

[c] Eviction rate/daily eviction rate/proportion of nest losses due to eviction.

Appendix 2. Literature data on nest predators in European and North American woodpeckers. Prey species: GiW: gila woodpecker (*Melanerpes uropygialis*), for other abbreviations *see* Table 1. Prey type: e = eggs, n = nestlings, a = adults in the nest. Predator species from the same continent are shown in systematic order.

Predator species	Prey species	Prey type	Location	Source
Europe				
Great spotted wodpecker (*Dendrocopos major*)	LSW	n	G. Britain	Tracy (1933)^{1*}, Brown (1976)^{1*}
Unspec. woodpecker	MSW	n	Switzerland	Pasinelli (2001)^{2}
Redstart (*Phoenicurus phoenicurus*)	GSW		G. Britain	Michalek & Miettinen (2003)^{3}
European starling (*Sturnus vulgaris*)	GSW	e, n	G. Britain	Michalek & Miettinen (2003)^{3}, Smith (2005)^{3}, Kosinski & Ksit (2006)^{3}
Jackdaw (*Corvus monedula*)	BW		Sweden	Nilsson *et al.* (1991)^{3}
European red squirrel (*Sciurus vulgaris*)	BW	e	Germany	Lange (1996)^{2}
Martens (*Martes martes, M. foina*)	BW	e, n	Sweden, Norway, Germany	Nilsson *et al.* (1991)^{2}, Lange (1996)^{2}, Rolstad *et al.* (2000)^{2}, Del Hoyo *et al.* (2002)^{3}
	GSW	n	Czech Rep.	Misík & Paclík (2007)^{2}
Unspec. carnivorous mammal	W-bW	n	Poland	Wesołowski (1995)^{2}
	MSW	n	Switzerland	Pasinelli (2001)^{2}
North America				
Black rat snake (*Elaphe obsoleta*)	NF	n	Iowa	Jackson (1970)^{1}
	R-bW	e, n	Illinois	Stickel (1962)^{1}
Unspec. snake	R-bW, R-hW, R-nS, Y-bS			Del Hoyo *et al.* (2002)^{3}
Red-headed woodpecker (*Melanerpes erythrocephalus*)	R-bW, R-cW		N. Carolina	LaBranche & Walters (1994)^{3}, Del Hoyo *et al.* (2002)^{3}
Red-bellied woodpecker (*Melanerpes carolinus*)	R-cW	n	Texas, Mississippi, N. Carolina	LaBranche & Walters (1994)^{3}, Rudolph *et al.* (1990)^{3}, Hazler *et al.* (2004)^{3}
Pileated woodpecker (*Dryocopus pileatus*)	R-bW			Del Hoyo *et al.* (2002)^{3}
House wren (*Troglodytes aedon*)	R-nS	e, n	B. Columbia	Walters & Miller (2001)^{2}
European starling (*Sturnus vulgaris*)	NF	a, e, n	Virginia, Maryland, Massachusetts, B. Columbia	Shelley (1935)^{2}, Howell (1943)^{1}, Dennis (1969)^{3}, Short (1979)^{3}, Wiebe & Swift (2001)^{3}, Wiebe (2003)^{2}, Del Hoyo *et al.* (2002)^{3}
	LW	e	Colorado	Vierling (1998)^{2}, Saab & Vierling (2001)^{3}
	GiW	n	N. Mexico	Brenowitz (1978)^{2}
	R-bW			Del Hoyo *et al.* (2002)^{3}
Deer mouse (*Peromyscus maniculatus*)	R-nS, NF	e	B. Columbia	Walters & Miller (2001)^{1}
Red squirrel (*Tamiasciurus hudsonicus*)	NF	a	B. Columbia	Howell (1943)^{3}, Wiebe & Swift (2001)^{3}, Fisher & Wiebe (2006a)^{1}
	Y-bS		N. Brunswick	Erskine & McLaren (1972)^{3}

Southern flying squirrel (*Glaucomys volans*)	R-cW	e	N. Carolina	LaBranche & Walters (1994)[3]
Northern flying squirrel (*Glaucomys sabrinus*)	B-bW		Oregon	Dixon & Saab (2000)[3]
Unspec. squirrel (*Tamiasciurus* sp.)	R-nS			Del Hoyo *et al.* (2002)[3]
Unspec. squirrel (family Sciuridae)				Short (1979)[3]
American marten (*Martes americana*)	NF		B. Columbia	Fisher & Wiebe (2006a)[1]
American mink (*Mustela vison*)	NF		B. Columbia	Wiebe & Swift (2001)[3]
Fisher (*Martes pennanti*)	NF		B. Columbia	Wiebe & Swift (2001)[3]
Long-tailed weasel (*Mustela frenata*)	NF		B. Columbia	Fisher & Wiebe (2006a)[1], Wiebe & Swift (2001)[3]
	WS		Colorado	Crockett & Hansley (1977)[1]
Unspec. mustelid (*Mustela* sp.)	R-nS	a, n	B. Columbia	Walters & Miller (2001)[2], Del Hoyo *et al.* (2002)[3]
	NF, HW, Y-bS	a, n	B. Columbia, N. Brunswick, N. Hampshire	Erskine & McLaren (1972)[3], Kilham (1977a)[2], Walters & Miller (2001)[2]
Raccoon (*Procyon lotor*)	Y-bS	a, n	N. Hampshire	Kilham (1971, 1977b)[2]
Black bear (*Ursus americanus*)	NF	a, n	Colorado, B. Columbia, N. Brunswick	DeWeese & Pillmore (1972)[2], Erskine & McLaren (1972)[3], Walters & Miller (2001)[2], Wiebe & Swift (2001)[3], Fisher & Wiebe (2006a)[3]
	Y-bS	n	Arizona, N. Brunswick	Franzreb & Higgins (1975)[2], Erskine & McLaren (1972)[3]
	WS	a	B. Columbia	Walters & Miller (2001)[2]
Domestic cat (*Felis cattus*)	NF	n	Massachusetts	Dennis (1969)[2]

[1] Directly observed or videotaped predators (*predation attempt interrupted by an observer).
[2] Predators confirmed indirectly from tracks at the robbed nest.
[3] Predators stated as confirmed in the literature without description.